

MUS. COMP. ZOOL.  
LIBRARY

MAR 18 1985

Harvard  
University

# B R E V I O R A

## Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 7 SEPTEMBER 1984

NUMBER 478

### NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA.

#### III. TWO NEW SEMIAQUATIC ANOLES FROM ANTIOQUIA AND CHOCÓ, COLOMBIA.

ERNEST E. WILLIAMS<sup>1</sup>

**ABSTRACT.** Two new semiaquatic anoles from Colombia, partly sympatric, and sometimes syntopic, prove to belong to distinct lineages despite convergence in habits and habitat. The larger of the two—*A. maculigula*, new species—belongs to the alpha section of the genus *Anolis* and the *eulaemus* subgroup of the *A. aequatorialis* species group. It is confined, so far as known, to the Departamento Antioquia and apparently to larger streams. The smaller species, *A. rivalis*, new species, is a beta anole of the *lionotus* species group and tends to prefer smaller streams and extends beyond the known range of *A. maculigula* in Antioquia and in Chocó.

In 1968 Norman J. Scott, collecting on a tributary of the Río Arquía in western Antioquia, Colombia, obtained a large anole of aquatic habits which he thought resembled *A. aquaticus*. It proves, however, to be a new species belonging to the alpha section of the genus. Syntopic with this species was a smaller form which Scott recognized as a member of the *lionotus* species group (beta section). This also proves to be new. These specimens were deposited in the collections of the Los Angeles County Museum (LACM).

Since these first collections, additional material of both species has been obtained in another area of western Antioquia some 70 km farther north by Juan Manuel Renjifo and Vladimir Corredor (material in the Instituto de Ciencias Naturales, Bogota [ICN]). Specimens of the larger species have been collected at Urrao, Parque Las Orquídeas, ca. 50 to 60 km east of the type locality, by

<sup>1</sup>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Horatio Echeverri for Marco Serna (collection of Colegio San José, Medellin (CSJ). Specimens of the smaller species have been collected in the Chocó independently by Philip Silverstone (MCZ) and Charles Myers (ICN). A further Chocó specimen of the smaller species has been found in the collections of the San Diego Natural History Society (SDSNH) collected by C. B. Perkins.

The larger new anole may be named, with reference to its heavily spotted throat:

*Anolis maculigula*, new species  
(Figs. 1-3)

*Holotype*: LACM 42150, adult male.

*Type locality*: Quebrada San Lorenzo, tributary of the Río Arquía near the small town of Belén ( $6^{\circ} 15'N$   $76^{\circ} 39'W$ ), about 10 to 15 km upstream from the junction of the Río Arquía with the Río Atrato, western Antioquia, Colombia, N. J. Scott coll., 17 April 1968.

*Paratypes*: Antioquia: LACM 42142, 42144-49, 42151-54, same data as the type; ICN 5917, Camp Pegadorcito (Ingeominas), (about  $6^{\circ} 42'N$   $76^{\circ} 27'W$ .) on the height of the Cordillera Occidental between Frontino on the south and Dabeiba on the north, Río

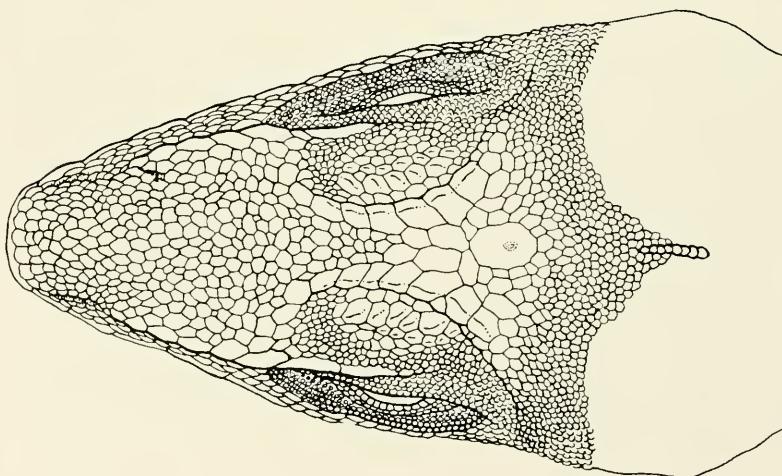


Figure 1. *Anolis maculigula*, new species. Type, LACM 42150. Dorsal aspect of head.

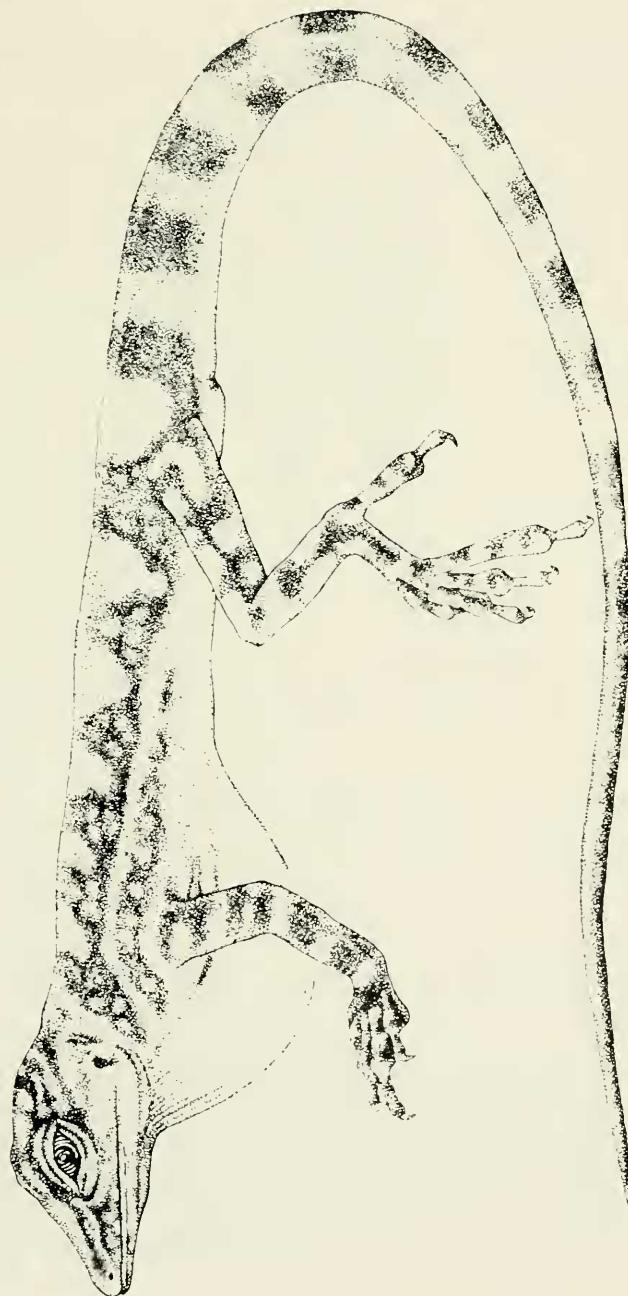


Figure 2. *A. maculigula*, new species. Type, LACM 42150. Lateral view of whole animal.

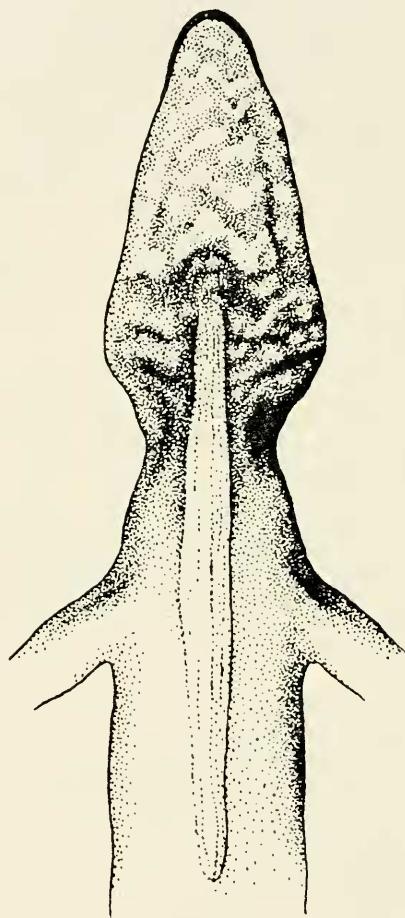


Figure 3. *A. maculigula*, new species. Type, LACM 42150. Throat pattern.

Amparradó, 805 m elevation, Juan M. Renjifo and Vladimir Corredor coll., 16 September 1981; ICN 5918, at the first stream beyond Pegadorcito, J. M. Renjifo and V. Corredor coll., 14 September 1981; CSJ 308-309, Urrao, Parque Las Orquídeas, Horatio Echeverri coll., 21 May 1981; CSJ 431, 445, 447, Urrao (Río Calles), Marco A. Serna and Horatio Echeverri coll., 10-12 July 1983.

*Diagnosis.* An alpha anole of moderate size related to *A. eulaemus* Boulenger and, like the latter, having small head scales and narrow digital dilations, but differing in having fewer scales between the supraorbital semicircles and between the semicircles and the interparietal, differing also in color, habits and habitat.

*Description. Head.* Head scales small, pustulose, swollen, keeled. Twelve to 19 scales between the second canthals. Eight to 11 scales bordering rostral posteriorly. Anterior nasal separated from rostral by one or two scales.

Two to three scales between supraorbital semicircles. A few supraocular scales distinctly enlarged, no well-defined supraocular disk. One to two elongate supraciliaries on each side followed by granules. Canthus distinct, seven canthal scales, the second longest. Eight to 11 loreal rows, scales small, subequal.

Temporal and supratemporal scales granular. A very indistinct double row of enlarged granules at margin between temporal and supratemporal areas. Scales around interparietal enlarged, interparietal larger than or about equal to ear, separated from supraorbital semicircles by one to three scales on each side or in contact.

Suboculars separated from supralabials by one row of scales, posteriorly grading into temporal granules, anteriorly diminishing gradually in size in front of eye. Seven to ten supralabials to center of eye.

Mentals wider than deep, in straight line contact with eight to ten scales between infralabials, grading in size from the infralabials toward the center. Sublabials not clearly differentiated. Central gular scales small, swollen, even conical, grading laterally into much larger scales.

*Trunk.* Two to three middorsal rows slightly enlarged, tricarinate, imbricate, grading into small, keeled but juxtaposed flank scales, showing small granules between them. Ventral scales equal to or smaller than the middorsals, smooth, flat or swollen, subimbricate or juxtaposed, sometimes showing small granules.

*Dewlap.* Large in male, extending onto first third of belly. Edge scales ca. equal to ventrals. Lateral scales in rows, several scales across, widely separated by naked skin. Barely indicated in female.

*Limbs and Digits.* Largest arm and leg scales larger than ventrals and uni- to multicarinate. Supradigital scales multicarinate. Sixteen to 22 lamellae under phalanges ii and iii of fourth toe.

*Tail.* Distinctly compressed to very strongly compressed, most strongly in the adult male, a low crest of unicarinate scales, the crest scales at least 2X those of the lateral rows. The other caudal scales uni- to multicarinate. No enlarged postanals in male.

*Size.* The male type measures 98 mm snout to vent. A topotypic male measures 72 mm, while the largest topotypic female is 73 mm snout-vent length. The male from Urrao (CSJ 308) is 107 mm snout to vent; the unregenerated tail is 215 mm long. The female (CSJ 309) from the same locality has 75 mm snout-vent length.

*Color in Life.* Normal Scott has provided notes from life for topotypic specimens. "Adult male: Dorsum with an obscure pattern of five dark brown blocks separated by lighter gray brown areas and broken by, on each side, a dorsolateral stripe of the same color. Dorsal crest paler and green. Tail and legs banded with dark gray brown and light gray green. On flanks a mixture of olive gray and orange flecks on a green ground. Side of head a mixture of orange and gray flecks, lips mottled and with blue flecks. Soles of feet olive brown. Throat with a series of orange and blue stripes. Chin mottled with orange, blue and gray, the blue predominant. Iris as in female but white ring tinged with green. Dewlap color complex: base with orange stripes on a blue gray ground, anterior third pale bluish rose, posterior portion white becoming pale blue toward belly. Juveniles colored much as females but green brighter on head, neck and sides. Adult female: Dorsum dark gray brown with gray black bar, lighter areas on neck, head and legs greenish gray. Sides mottled gray, olive green and black with a few light gray punctations. Side of head mostly greenish. Venter clear white, throat mottled green and white, underside of head patterned with white and gray, the chin with green and gray. Iris dark brown enclosing a narrow white ring."

Juan Renjifo in a note to Stephen Ayala reports the color in life of the Amparradó *maculigula* (translated): "Color green (lichenate) with dark blotches on the back, the first above the shoulders. A blotch at the shoulder dark with a white spot in the center."

*Color in Preservative.* Color now differs substantially from that reported for the fresh specimens. All blues, pinks and greens are gone. There are only light and dark grays but the complex pattern is retained. The dark crossbars of the middorsum contain light spots and the lower flanks tend to be vermiculate. The throat is boldly to weakly vermiculate, less strongly vermiculate in males than in

females, in which the heavily marked throat contrasts strikingly with the light and unmarked belly. The skin of the throat fan is gray.

*Habitat and Habits.* The type locality, Quebrada San Lorenzo, is described as a stream about 10 m wide with occasional waterfalls, with a moderately steep gradient and huge boulders. *A. maculigula* was most common where there were 3 to 4 m diameter moss-covered boulders at the head of pools, when first seen most were on the upstream vertical face of the boulders in the spray zone and tried to escape under the overhanging edge of the boulders. In Quebrada San Lorenzo the smaller (*lionotus* group) species also occurred but was less common. (See further below.) No comparable details are available for the habitat of ICN 5917 and 5918, but the latter specimen is reported as on rocks in a stream.

*Comparisons.* *A. maculigula* is clearly an alpha anole; a caudal vertebra dissected from a broken tail shows no trace of transverse processes. It is referred to the *aequatorialis* species group on the basis of very small head scales, large size and narrow digital dilations. Since its toe pads are "raised," i.e., overlap distally the proximal scales under the first phalanx, it is further referred to the *eulaemus* subgroup in contrast to species with pads "not raised," i.e., not overlapping but continuous with the scales of the first phalanx. (The latter are the *aequatorialis* subgroup.)

Within the *eulaemus* subgroup, in which there are a confusing number of undescribed populations, *A. maculigula* is distinctive in its pustulose head scales, its small ventrals, usually smaller than the small dorsals, and in the relatively large size of the interparietal which is almost always larger than the ear, in the very compressed tail and in a distinctive coloration. It may well be unique among the known eulaemoid forms in its semiaquatic habits also. Certainly no other member of the group shows so compressed a tail or *maculigula*'s tendency to a lined pattern.

The second and smaller species may very appropriately receive the Latin name that means "user of the same stream":

*Anolis rivalis*  
(Figs. 4-7, 12, 14)

*Holotype:* LACM 42124, adult male.

*Type locality:* Belén, Río Arquía, Antioquia, Colombia (6° 15'N, 76° 39'W), Norman J. Scott coll., 17 April 1968.

*Paratypes:* Antioquia: LACM 42128-133, 42135, 42137-139, MCZ 115720-722 from the type locality, Norman J. Scott coll.; LACM 42125-127, 42141, 45002-07, 51540, Finca Los Llanos, Río Arquía, Philip Silverstone coll., 1968; ICN 5912, Camp Pegadorcito (Ingeominas), 45 minutes by helicopter from Medellín, on the height of the Cordillera Occidental between the towns of Frontino to the south and Dabeiba to the north, Río Amparradó, 805 m elevation, (about  $6^{\circ} 42'N$ ,  $76^{\circ} 27'W$ ), Juan M. Renjifo and Vladimir Corredor coll., 13 September 1981; ICN 5913, Filo Amparradó, the same area and collectors, 16 September 1981; ICN 5914, Camp Chontaduro, same area and collectors, 9-12 September 1981; ICN 5915, same area and collectors, 14 September 1981. Chocó: LACM 72766, 72772, MCZ 100353, Alto de Buey, P. Silverstone coll., 1968; ICN 4053, Quebrada Mutatá, 200 m, northern base of Alto de Buey, C. W. Myers, John Daly and Michael G. A. Hill coll., 18-24 October 1978; SDSNH 31163, "Port Utria," = Puerto Utria ( $6^{\circ} 02'N$ ,  $76^{\circ} 23'W$ ), C. B. Perkins coll., 25 February 1938.

*Diagnosis.* A member of the *lionotus* group of beta anoles, differing from the remainder of the group in the combination of small but not minute head scales (13 to 18 across snout between second canthals), one to two rows of scales between the supraorbital semicircles, interparietal in contact with the semicircles or separated by no more than two rows of scales, and by a zone of moderately large, indistinctly keeled, flat scales on the middorsum in 11 to 18 rows.

*Description. Head.* Scales small, uni- to multicarinate. Thirteen to 18 scales across snout between second canthals. Seven to nine scales border rostral posteriorly. Anterior nasal scale separated from rostral by one scale. Nine scales between supranasals. Scales in posterior portion of frontal depression smaller than those anteriorly placed.

Supraorbital semicircles separated medially by one to three scales, in contact laterally with the largest scales of the supraocular disks which consist of a variable number of wrinkled or keeled scales, a few of which may be much larger than the others. One to three elongate supraciliaries continued posteriorly by a series of smaller scales. Canthus distinct, canthals 9. second largest. Six to 10 loreal rows, lowermost largest.

Temporals small and flat, not granular. A distinct double supratemporal row, dorsad of which nearly granular scales grade

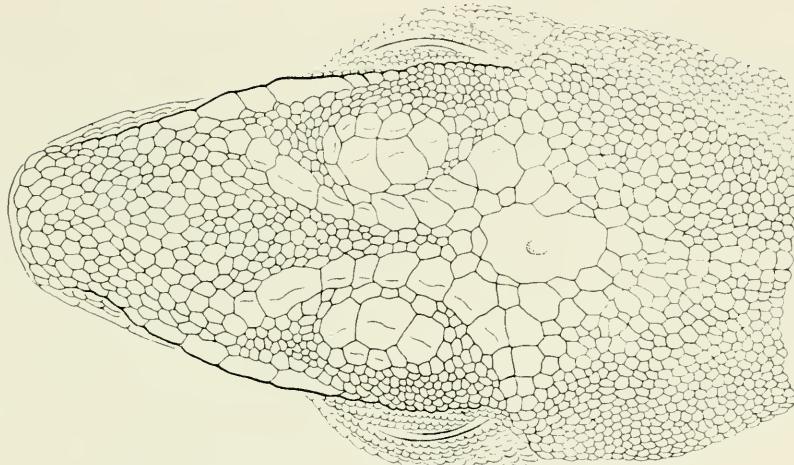


Figure 4. *A. rivalis*, new species. Type, LACM 42124. Dorsal aspect of head.

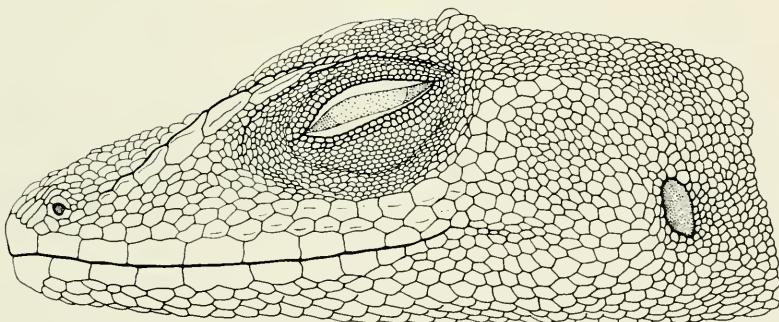


Figure 5. *A. rivalis*, new species. Type, LACM 42124. Lateral aspect of head.

into the flat scales surrounding the large interparietal, usually larger than ear and in contact with the semicircles or separated by one to two scales. Scales posterior to interparietal not different in size from middorsals but grading into smaller nape scales which then grade posteriorly into the dorsals. Suboculars weakly keeled, narrowly in contact with supralabials or separated by one scale row, grading

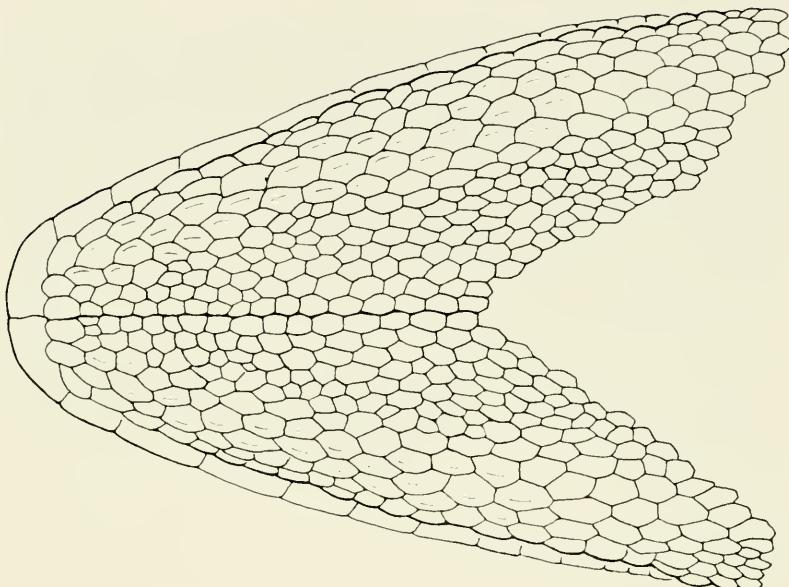


Figure 6. *A. rivalis*, new species. Type, LACM 42124. Ventral view of chin.

anteriorly into loreals, posteriorly more sharply distinct from the temporals. Six to nine supralabials to the center of the eye.

Mental divided, wider than long, in contact with six or seven scales between infralabials. Gular scales smallest medially, quadrate, swollen.

*Trunk.* Middorsal scales flat, hexagonal, wrinkled, in ca. 11 to 17 rows, grading quite gradually into subgranular flank scales, larger in the center of the body than on the nape, becoming slightly smaller again in the sacral region and on the base of the tail. Ventrals smaller than dorsals, keeled, imbricate.

*Dewlap.* Moderate, extending onto first third of belly, lateral scales weak, in densely packed rows, edge scales keeled, slightly larger than ventrals.

*Limbs and Digits.* Scales on limbs strongly unicarinate except at knees and elbows where they are multicarinate. Supradigital scales multicarinate. Twelve to 18 scales under phalanges ii and iii of fourth toe.

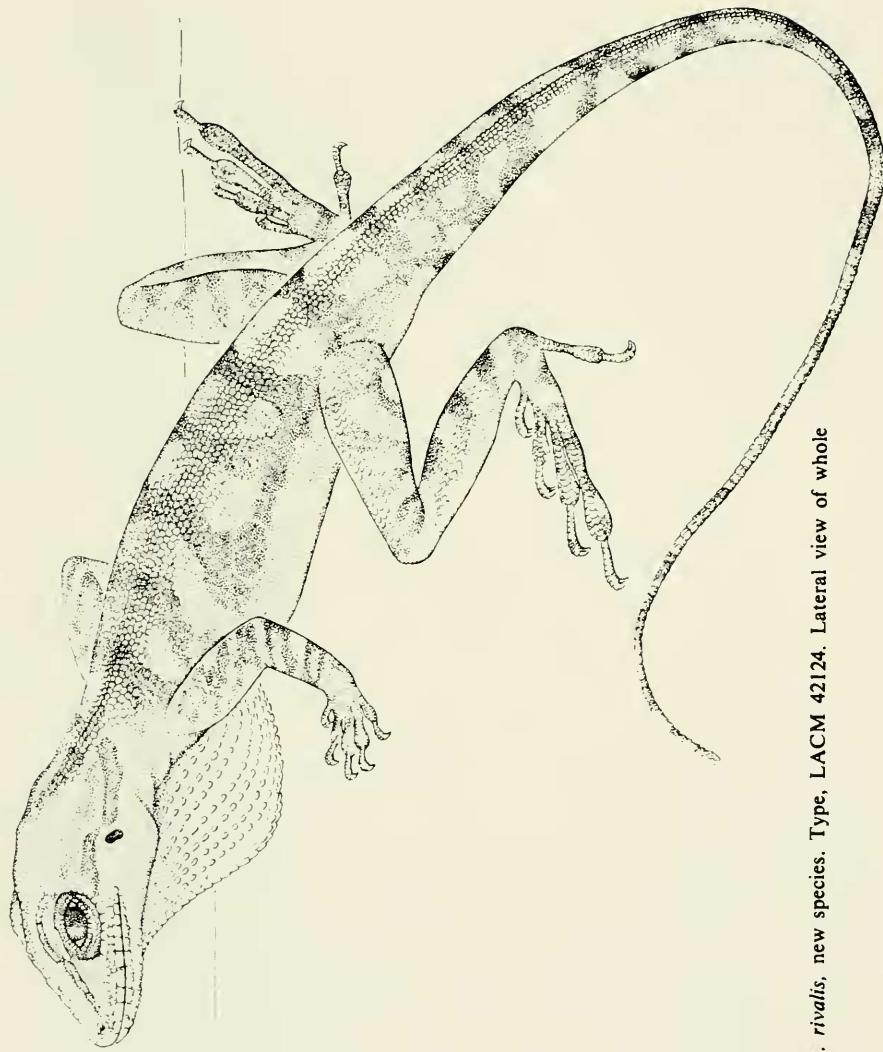


Figure 7. *A. rivularis*, new species. Type, LACM 42124. Lateral view of whole animal.

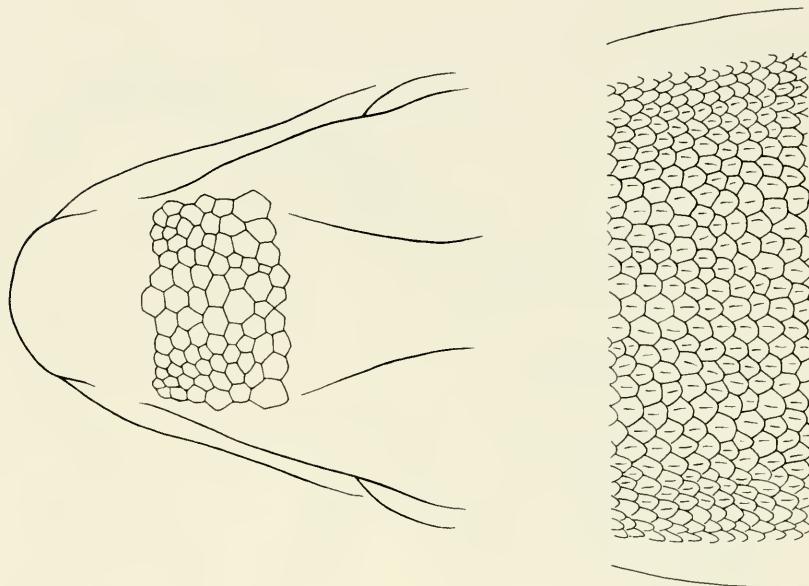


Figure 8. *A. oxylophus*, KU 34262. Frontal and middorsal scales.

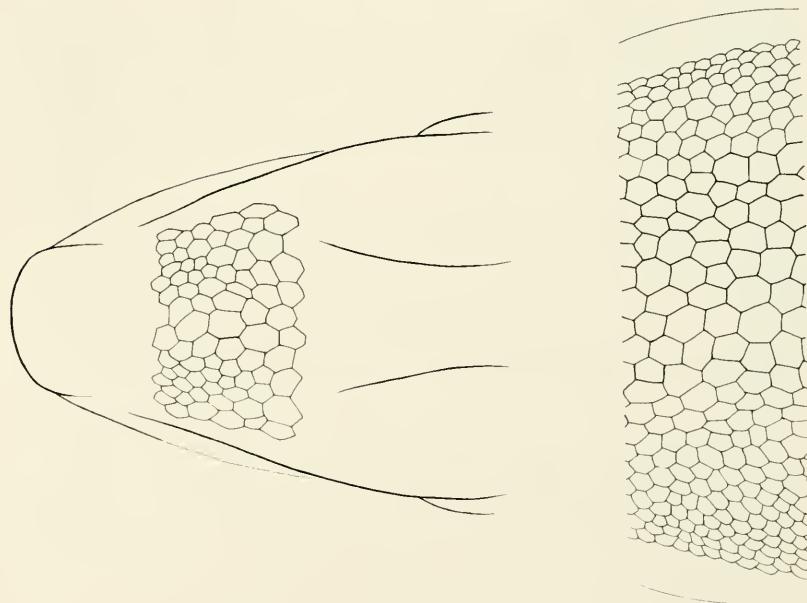


Figure 9. *A. lionotus*, KU 75951. Frontal and middorsal scales.

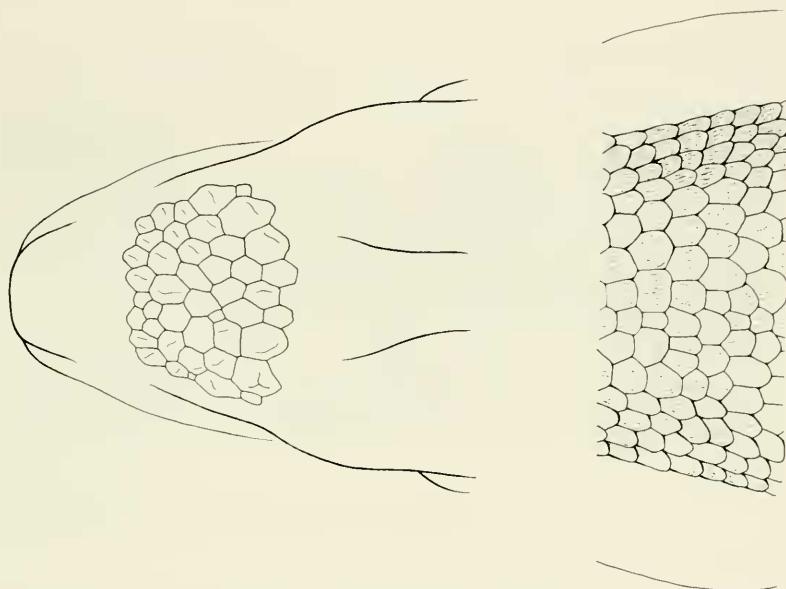


Figure 10. *A. macrolepis*, MCZ 133000. Frontal and middorsal scales.

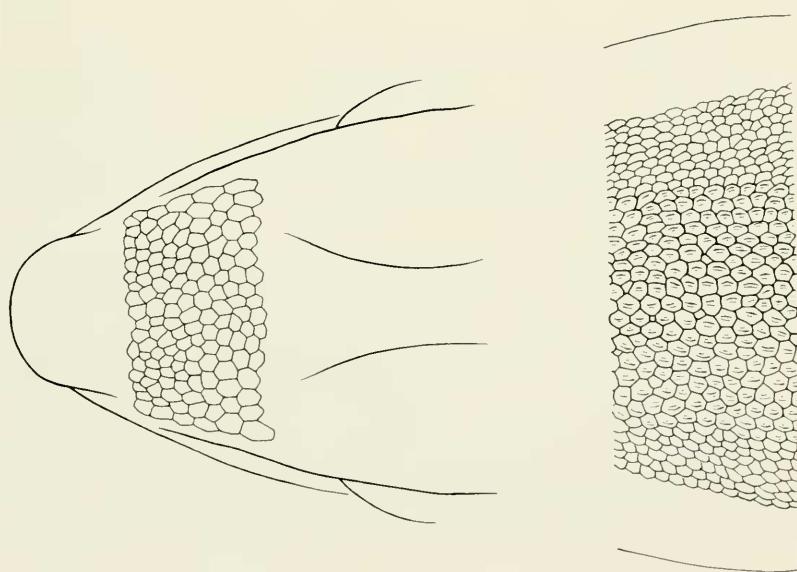


Figure 11. *A. poecilopus*, KU 113249. Frontal and middorsal scales.

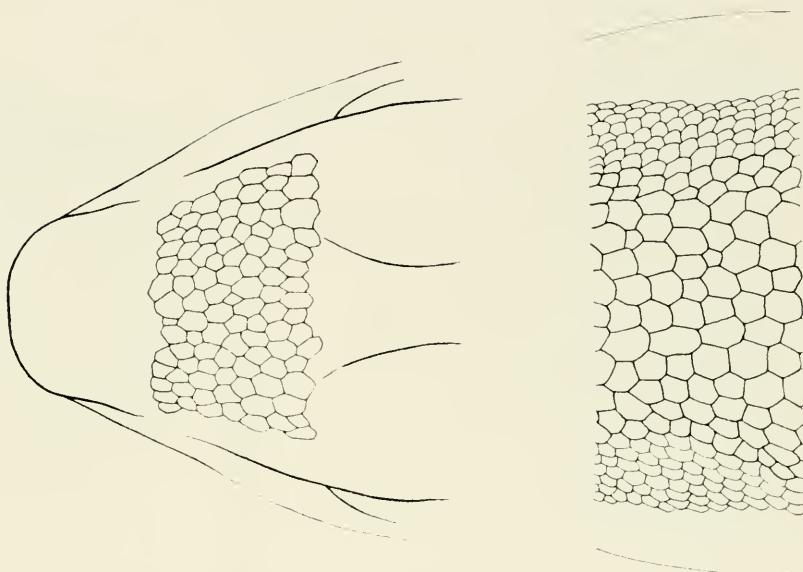


Figure 12. *A. rivalis*, LACM 42129. Frontal and middorsal scales.

*Tail.* Compressed without dorsal crest. Verticils indistinct. Enlarged postanals absent.

*Color as Preserved.* Brown with darker flanks. Middorsum banded. Two narrow light lines on sides, one above shoulder, one starting at axilla. Spotting on lower flanks. Limbs banded. Belly and throat white or very weakly spotted. Dewlap white. Nape white to above level of ear where a darker margin sets it off against the dorsal light brown.

*Size.* The type male is 62 mm in snout-vent length. MCZ 115722 and LACM 42138, topotypic males, are each 64 mm snout to vent.

*Color in Life.* Scott provides color notes on the topotypic specimens: "Adult male: Dorsum dark brown with thin green brown vertical bands on flanks. Several stripes from axilla to groin, the lower ones heavily suffused with red. Light areas on sides dusty rose. Venter yellowish white with heavy red suffusion on sides of abdomen, throat and underside of head. Iris dark chestnut enclosing a narrow yellow ring. Dewlap solid orange. Adult female: Dorsum



Figure 13. *A. rivalis* from Quebrada Mutatá, 200 m, northern base of Alto del Buey, Chocó, Colombia. Photo by C. W. Myers.

as in male but with only a faint hint of red suffusion. Light areas of head white becoming green on snout. Venter yellowish white. Dewlap area with pale orange spot, throat anteriorly white. Iris as in male."

Notes by C. W. Myers on the specimen obtained from Quebrada Mutatá record the following colors: "Brown, changeable to brownish green, with lateral line and lower side of neck dirty white. Throat gray, dewlap light orange, venter greenish gray. Iris brown. Tongue light gray."

Juan Manuel Renjifo has supplied color notes on ICN 5912 from the Río Amparradó region: Greenish brown with bars of lighter greenish brown forming chevrons on the middle of the back. Labials and flanks rosy salmon. Venter yellowish cream. Gular sac white.

One entry in Scott's field notes cites an unspecified *rivalis* from Belén as having an orange dewlap. There would appear to be a range of dewlap colors in this species.

*Habitat and Habits.* At Quebrada San Lorenzo, Scott reports *A. rivalis* both to be less common and to occur on small rocks near the bottom of pools rather than on the huge moss covered boulders preferred by *A. maculigula*. They escaped by running from rock to rock over the water surface. Some were taken at night sleeping on

vegetation overhanging the stream. He specifically mentions (letter of February 28, 1979): "Quebrada San Lorenzo was the only place where I got both aquatic species. Nearby Quebrada Barrero had less water and seemed to have only the "lionotus" [= *rivalis*] type."

The single specimen of *A. rivalis* obtained by the Myers group in 1978 was again found in a quebrada, but the notes do not cite any larger aquatic species.

Renjifo in his field notes does not mention close or co-occurrence of the two species and confirms the semi-aquatic habits of *rivalis* in the Amparradó region. He cites ICN 5912 as (translated) "in forest on trunk above the stream, ½ meter above ground level;" ICN 5914 "in stream on a stone;" ICN 5915 "sleeping on rocks in the stream alongside the current;" and ICN 5918 "in stream....on rocks."

*Comparisons.* *A. rivalis* is a member of the beta series and of the *lionotus* species group.

The latter is a series of taxa (the other referred species: *oxylophus* Cope, 1875, *lionotus* Cope, 1861, *poecilopus* Cope, 1862, *macrolepis* Boulenger 1911) that extend from Nicaragua to Ecuador, replacing one another with minimal or no overlap, so far as known. A sixth taxon belonging to this group occurs in northwestern Ecuador and southwestern Colombia. It will be described by Kenneth Miyata. All are characterized ecologically by "aquatic" habit and riparian habitat and (usually) by a zone of enlarged dorsal scales, more or less similar in size over an area of 14 to 20 rows, then grading laterally into the flank scales. They have also small keeled ventrals and a more or less well developed flank stripe.

The species of this group ring the changes on just a few morphological characters: the size of the head scales, the number of scale rows between the supraorbital semicircles, the number of scales between the interparietal and the semicircles, the size of supratemporal and nape scales, and the size and also the keeling or lack of keeling of the middorsals. Each of these characters varies independently, and adjacent species tend to be sharply distinct in one or more features.

No revision of the *lionotus* species group exists nor has South American *macrolepis* been recognized as a member of it until recently (Williams, 1976).

Boulenger (1911) in describing *macrolepis* did, indeed, associate it with *poecilopus* but also suggested a relationship to *notopholis* (*humilis* species group), to which it is only superficially similar.

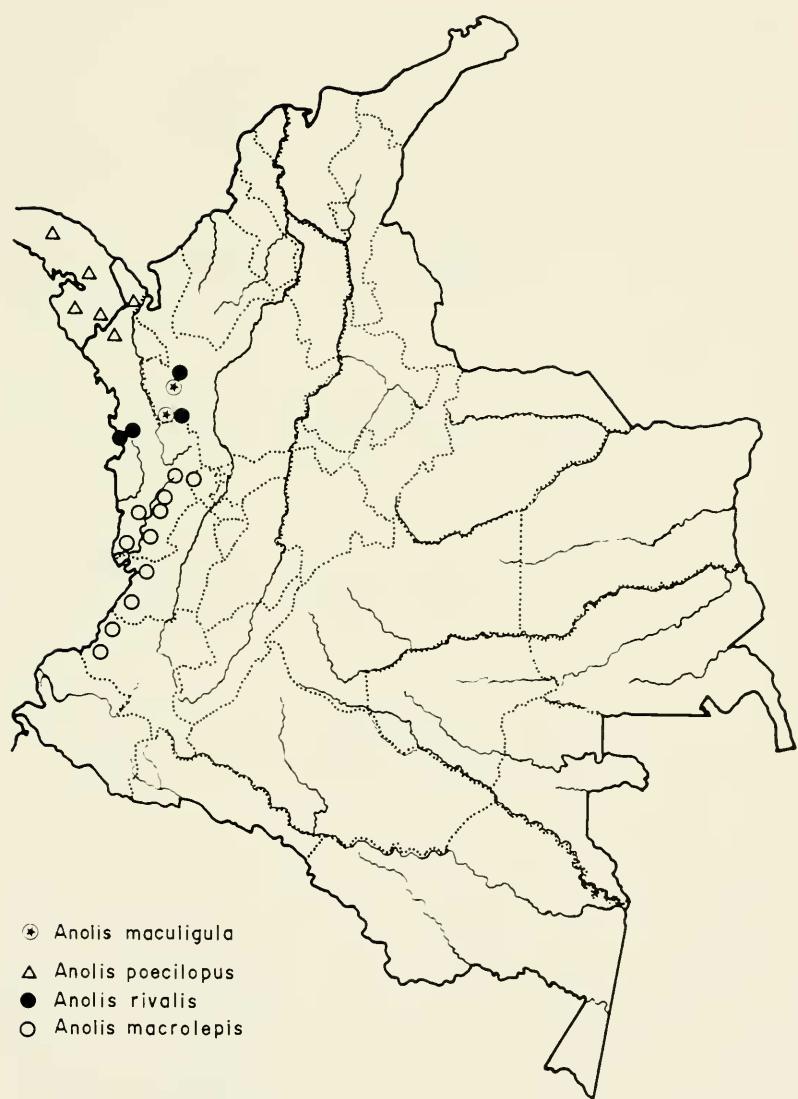


Figure 14. Map: Localities for semiaquatic anoles in Colombia and adjacent Panama.

Table 1. Scale characters within the *Anolis lionotus* species group.

	<i>oxylophus</i> (Costa Rica, Nicaragua)	<i>lionotus</i> (Panama)	<i>poecilopus</i> (Panama, Colombia)	<i>macrolepis</i> (Colombia)	<i>rivalis</i> (Colombia)
head scales	moderate	moderate	minute	moderate	small
number of scales between second canthals	8-14	8-12	14-21	7-10	13-18
supraocular scales	moderate to <i>large</i> , keeled	moderate to <i>large</i> , keeled	moderate, keeled	large, wrinkled	moderate, wrinkled
scales between semicircles interparietal/ear	1-3	ca. =	1-3	2-5	0-2
circum-interparietal scales	<i>large</i>	<i>moderate</i> <i>to large</i>	anteriorly moderate <i>to large</i>	large moderate to small, posteriorly <i>minute</i>	ca. = or > moderate to large

number between ip and semicircles	1-3	1-2	2-5	0-2	0-2
supratemporal scales	large	moderate	minute	moderate to large	small to moderate
nape scales/ dorsals	=	(<)	< smaller than small dorsals	=	distinctly <
dorsal zone of enlarged scales	moderate, flat, weakly keeled, or smooth, weakly imbricate	large, flat, smooth, juxtaposed	small with raised edges and central keel	large, keeled or wrinkled, weakly imbricate	large, keeled or wrinkled, weakly imbricate
number of enlarged dorsal rows	19-22	11-16	13-24	11-17	8-15
dorsal scales/ ventrals	ca. =	ca. 2x >	ca. =	>	>
lamellae 4th toe	13-17	14-16	12-19	13-16	12-18
adult male size	72	73	68	62	64

Taylor (1956) in his discussion of the lizards of Costa Rica called attention to the discrepancies between the type description of *lionotus* Cope, 1861 (with a type locality in Panama) and that of *oxylophus* Cope, 1875 (without exact locality but presumably from Costa Rica), which was supposedly a synonym. However, lacking Panamanian specimens, he followed then and current usage in applying the name *lionotus* to Costa Rican animals. My own examination of most of the material available in American museums shows significant differences between eastern Panamanian and western Panamanian and Costa Rican-Nicaraguan specimens. Campbell (1973) noted the character of true *lionotus* that has most impressed me: dorsal scales about twice the size of the ventrals. In *oxylophus* (as in *poecilopus*) the dorsals and ventrals are about equal but in *poecilopus* the dorsals are strongly keeled, in *oxylophus* smooth or weakly keeled. Table 1 reports the characters distinguishing members of this group.

The new species is distinguished from all other members of the *lionotus* group by a combination of characters: small but not minute head scales, few scales between the supraorbital semicircles, small to moderate supratemporal scales, nape scales distinctly smaller than the enlarged dorsals which are large, larger than the ventrals, wrinkled or weakly keeled and weakly imbricate. From *poecilopus* it is distinguished by its much larger middorsals, fewer rows between the supraorbital semicircles and its larger circum-interparietal scales. From *macrolepis* it is distinguished by its somewhat larger middorsals, the nape scales distinctly smaller than the large middorsals (rather than subequal) and by smaller head scales.

*Discussion.* The sympatric occurrence of two semiaquatic anoles is not unique: within the *lionotus* group there is the example of the local sympatry of *poecilopus* and *lionotus* in the vicinity of the Panama Canal (Campbell, 1973). In this case the overlap zone is suspected to be narrow, but knowledge of the distributions is not adequate to demonstrate this. In the case of *poecilopus* and *lionotus*, the two overlapping species are very different within the group in dorsal and head scale size. (In general, in the *lionotus* group, although the species are primarily allopatric, the differences summarized in Table 1 are greater in adjacent than in distant taxa.)

The two sympatric semiaquatic species here described are quite different in their affinities, belonging to different sections of the genus *Anolis*. They are adequately different in scale characters but

not quite so strikingly as the most different species pairs *within* the *lionotus* group. The similarities in habits, in the pronounced flank stripes, and in the strongly compressed tails, are indeed more impressive than their differences.

But these similarities are parallels only and are seen in other semiaquatic anoles not at all closely related, as Schwartz has demonstrated in describing a taxonomically quite isolated semiaquatic anole from Hispaniola (Schwartz, 1978). The semiaquatic anoles, except for the allo-parapatric series that constitutes the *lionotus* group, are not at all a lineage, but only an ecomorph in the sense of Williams (1972, 1983).

#### ACKNOWLEDGMENTS

I am indebted to the curators who have provided me the opportunity to describe the new species: John Wright and Robert Bezy of the Los Angeles County Museum, Pedro Ruiz of the Instituto de Ciencias Naturales, Bogotá, Colombia and Gregory Pregill of the San Diego Natural History Society. Norman Scott and Charles Myers have allowed me to quote from their field notes, and Pedro Ruiz has transmitted the field localities and observations of Juan Renjifo and Vladimir Corredor. Stephen Ayala has commented on the manuscript and provided the map which compares the distributions of Colombian aquatic anoles. Laszlo Meszoly has done the illustrations. The photograph of *A. rivalis* was provided by Charles Myers.

#### LITERATURE CITED

BOULENGER, G. A. 1911. Description of new reptiles from the Andes of South America, preserved in the British Museum. Ann. Mag. Nat. Hist. ser. 8, **8**: 19-25.

CAMPBELL, H. W. 1973. Ecological observations on *Anolis lionotus* and *A. poecilopus* (Reptilia, Sauria) in Panama. Amer. Mus. Novitates, No. 2516, pp. 1-29.

COPE, E. D. 1861. Notes and descriptions of anoles. Proc. Acad. Nat. Sci. Phila., **1861**: 209-215.

\_\_\_\_\_. 1862. Contributions to Neotropical saurology. Proc. Acad. Nat. Sci. Phila., **1862**: 159-188.

\_\_\_\_\_. 1875. On the Batrachia and Reptilia of Costa Rica. J. Acad. Nat. Sci., **8**: 93-157.

SCHWARTZ, A. 1978. A new species of aquatic anole (Sauria, Iguanidae) from Hispaniola. Ann. Carnegie Mus., **47**: 261-279.

TAYLOR, E. 1956. A review of the lizards of Costa Rica. *Univ. Kansas Sci. Bull.*, **38**: 3-222.

WILLIAMS, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology*, **6**: 47-89.

\_\_\_\_\_. 1976. South American anoles: the species groups. *Pap. Avuls. Zool. S. Paulo*, **29**: 259-268.

\_\_\_\_\_. 1983. Ecomorphs, faunas, island size and diverse end points in island radiations of *Anolis* pp. 326-370, 481-484. *In* Huey, R., E. Pianka, and T. Schoener (eds.), *Lizard Ecology - Studies of a Model Organism*, Harvard University Press, Cambridge, Mass.